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# The Mycorrhizal Fungal Community with Special Reference to Nutrient Mobilization

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## INTRODUCTION

Great strides have been made towards an understanding of the structures of mycorrhizal roots and three major types, the ericoid, ecto- and vesicular arbuscular mycorrhizas are now recognized (Harley and Smith, 1983). However, we have relatively little knowledge of the function of each type of root and know even less of the relationship between the communities of fungi forming mycorrhizas and those containing saprotrophic and necrotrophic fungi, with which they must co-exist in the soil. The definitive difference between communities of mycorrhizal fungi and the other members of the soil microbiota is that, as mutualists, they have direct access to simple sugars in the form of photosynthate supplied by their autotrophic hosts. The fundamental requirement for fixed carbon amongst heterotrophic populations was probably the single most important factor leading to the selection of the mycorrhizal habit. It is a feature which critically influences the spatial and temporal distribution of mycorrhizal fungi in soil as well as the outcome of their interactions with other groups of fungi.

Since the differences between the various microbial communities in soil arise primarily from their distinctive modes of carbon acquisition it follows that a realistic understanding of mycorrhizal communities and of their interactions with other components of the soil microflora can only be obtained under circumstances in which the fungi are grown with their autotrophic partners in the absence of accessory supplies of free carbon. While we can learn something of the biochemical and physiological potentials of mycorrhizal fungi by growing them in cultures containing exogenous carbon, such experiments tell us little of the extent to which their potentials are expressed in the real world, or of their interaction with other groups of fungi. The factor above all others which has hampered progress towards an understanding of the mycorrhizal community has been the failure to develop methods enabling the growth and differentiation of the mycorrhizal mycelium to be examined non-destructively under conditions even remotely resembling those prevailing in the field. Studies on agar or on cellulose-based

media such as growth pouches (Fortin et al., 1980) go some way towards satisfying this requirement but, as pointed out by Bowen (1979), the only medium capable of providing us with real understanding of microbial interactions and growth processes around roots is the soil itself.

Recently, microcosms have been developed which permit the nondestructive analysis of the development and function of the mycorrhizal mycelia as they grow through unsterile soil from infected roots. By supplementing observations made under these semi-natural conditions with those from the field and from laboratory-based pure culture work a fuller picture of each of the different types of mycorrhizal community, is beginning to emerge. Unfortunately, the use of the new methods has not been extended to encompass analysis of interactions between the mycorrhizal and other fungal communities, although studies of this kind present exciting prospects for the future.

Each of three major types of mycorrhiza, is predominantly associated with a particular suite of soil conditions (Read, 1984a) which develops as a response to nutritional and climatic factors. Segregation of types thus occurs, heathlands containing communities dominated by plants with ericoid mycorrhizas predominating in soils of high latitudes and altitudes, ectomycorrhizal forests covering intermediate areas, these giving way to communities dominated by vesicular arbuscular mycorrhizal species in the warmer drier climates of low latitudes. The challenge is therefore to identify those structural, physiological and biochemical features of a given type of mycorrhizal community that have led to its selection under a given set of soil conditions. The evidence suggests the ability to mobilize nutrients has been of prime importance as a selective feature, there being a close correlation between the biochemical potential shown by mycorrhizal fungi and the chemical complexity of the nutritional resources in the soils that they inhabit.

## The Ericoid Mycorrhizal Community

Heathland ecosystems in the northern hemisphere occupy environments characterized both by extreme soil conditions in which accumulations of acidic 'mor' humus or peat restrict rates of nutrient turnover, and by low diversity of higher plant species. Dwarf shrub formations dominated by *Calluna vulgaris*, *Vaccinium*, *Erica* and *Gaultheria* spp. occur over millions of hectares of the tundra, as well as in the uplands of lower latitudes and in regions with Mediterranean climate, where they may be part of more diverse plant communities. These genera produce a mycorrhiza of uniform structure, the 'ericoid' type, the fungal component of which is inevitably of great significance in these ecosystems if only because of the overwhelming preponderance of its autotrophic hosts.

The first studies to combine isolation of fungal symbionts from ericoid roots with reinoculation (Doak, 1928; Friesleben, 1934; Bain, 1937) demonstrated that the endophytes of ericoid roots, when grown in agar culture, produced slow growing dark colored and normally sterile mycelia. Burgeff (1961) working in a wet heath confirmed these observations but also isolated a sporulating fungus which was identified as *Oidiodendron griseum*. This fungus has since been shown to form what appear to be typical ericoid mycorrhizas in *Vaccinium* (Couture et al., 1983) and a related species *O. maius* will infect *Rhododendron* (Douglas et al., 1989). Dark sterile isolates comparable with those described by the early workers have been induced to produce sexual structures in culture and the fungus is now known to be the Ascomycete, *Hymenoscyphus ericae* (Read, 1974). Notwithstanding the occasional appearance of *Oidiodendron* spp

among isolates from ericoid roots, strains of the *Hymenoscyphus ericae* type are by far the most widely occurring of the ericoid endophytes, and they are still the only fungi to have been shown, following reinoculation and analysis of growth responses of host plants, to be true mutualists (Read, 1983). It thus appears that, as is the case with the flowering plant communities, the mycorrhizal community of heathlands dominated by ericaceous plants is characterized by a low level of species diversity.

Intensive analysis of the biochemical potential of *Hymenoscyphus ericae* both in pure culture and in mycorrhizal association with its host has shown that this fungus has a spectrum of enzymic capabilities which adapt it superbly to the soil environments characteristic of its host plants. Many of the refractory compounds known to be characteristic and major constituents of mor humus and peat (Stevenson, 1982) can be lysed. Amongst these lignin (Haselwandter et al., 1990), chitin (Leake and Read, 1990b) and a range of phenolic compounds (Leake, 1987) including tannin (Leake and Read, 1990c) can be degraded, the products being assimilated as carbon sources.

As well as providing access to carbon, these phenol oxidase, lignase and chitinase activities will facilitate the unmasking of more labile organic materials in litter and humus. Perhaps of greatest importance among these are nitrogenous substrates, because nitrogen is known to be the main growth-limiting factor in heathland, boreal, and most temperate forest environments (Ellenberg, 1988), and since most of the nitrogenous resources are in some form of organic combination. Up to 20% of the total N in a Swedish pine-heath was shown by Bååth and Söderström (1979) to be localized in fungal mycelia. A combination of chitinolytic and proteolytic attack would provide access to this nitrogen. A vigorous proteolytic capability has been demonstrated in *Hymenoscyphus ericae* when grown both in pure culture and in mycorrhizal association with its host plant (Bajwa et al., 1985; Leake and Read, 1989, 1990a). It has been confirmed that the endophyte obtains nitrogen from protein even when the polymer is co-precipitated with tannin (Leake and Read, 1990c). Most importantly, the nitrogen assimilated by the fungus from such sources is transferred to the host plant (Bajwa et al., 1985; Read, 1987), which otherwise has no access to it.

Most of the phosphorus (P) reserves of heathland soil are also in organic combination and it has been shown (Mitchell and Read, 1981) that the mycorrhizal endophyte can mobilize P from inositol hexaphosphate precipitated with the metals aluminium and iron. Its acid phosphatase enzymes retain activity in the presence of ecologically realistic concentrations of these metals both of which are increasingly solubilized under acid conditions (Shaw and Read, 1989).

It is recognized that podsolic soils and peats of the kind which support ericoid communities have a characteristic flora of saprotrophic micro-fungi. Söderström and Bååth (1978) observed that in a given horizon the species composition of this flora was comparable in sites separated by large distances. In the horizons occupied by most of the mycorrhizal roots of ericaceous plants the most frequently isolated fungi were in the genera *Mortierella* and *Pencillium*. These microfungi were themselves subsequently shown to display a wide range of enzyme activities in pure culture (Bååth and Söderström, 1980). In view of this, it is clearly important to determine the relationships between the functional activities of such organisms and those of the mycorrhizal community.

It is probable that the outcome of these interactions will be determined by the definitive mode of carbon acquisition shown by the mutualists, and some experimental evidence supports this contention. Measurement of respiratory activity of soil taken

from *Calluna* heathland indicates that despite the presence, revealed in subsamples, of a saprotrophic population of fungi including genera such as *Mortierella*, *Trichoderma* and *Penicillium*, basal levels of $CO_2$ output are extremely low. These activities can be increased considerably by addition of glucose demonstrating that carbon availability is limiting the activity of the saprotrophs. Respiratory output of $CO_2$ is also raised significantly if a mycorrhizal plant of *Calluna* is grown in the otherwise unamended soil (Fig. 1.) That this activity is dependent upon supplies of current assimilate is confirmed by a reduction of $CO_2$ output observed when the *Calluna* shoot is excised or kept in darkness. While some of the increased respiratory activity of soil in the presence of *Calluna* can be attributed to the roots themselves, a considerable proportion must arise from the mycorrhizal fungus, which occupies up to 80% of the biomass of the infected root. Experiments such as this suggest strongly that the mycorrhizal community will be physiologically more active than any other provided that assimilate supplies are maintained. There is evidence in support of a 'priming' role for simple carbon sources from laboratory studies which show that proteinase activities are enhanced where the endophyte is supplied with 'starter' carbon of the kind that, in nature, would be supplied by the host.

It is not only the ability of the fungus to express enzyme potential but also that of the host to regulate these activities in such a way as to protect itself, which currently excites interest. In one of the key enzymes, proteinase, it is now known that regulation of both production and activity can be achieved simply by changes of hydrogen ion concentration (Leake and Read, 1990a). Activity of the enzyme is expressed only under the very acidic conditions typical of heathland soil. At pH 6.0 and above, which is close to that of the intracellular environment of the ericoid root, enzyme production and activity are both completely repressed. It remains to be seen whether the other

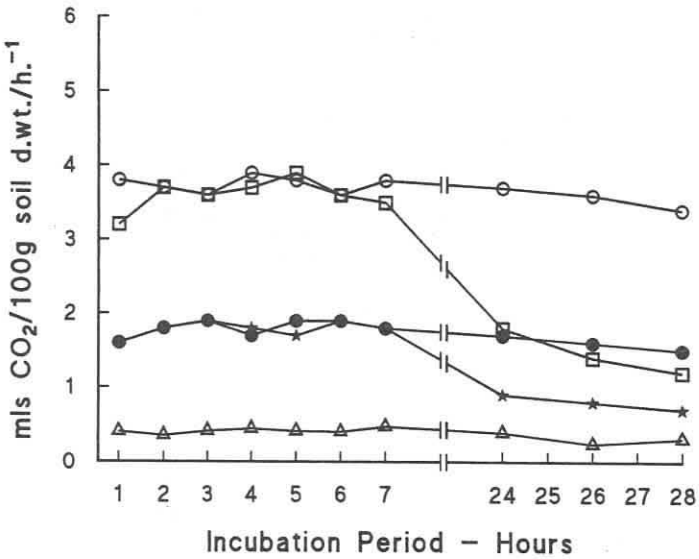



**Figure 1** Equilibrium rates of respiration of fresh *Calluna* raw humus (pH 3.5) measured at 15°C in the untreated condition (open triangles), after addition of 200 (open squares) or 400 (open circles) ppm glucose, and where untreated but supporting growth of rooted mycorrhizal plants of *Calluna* (closed circles) from some of which shoots were excised at 7 hours (closed stars). (From unpublished data of Fassi and Read).

enzymes of the ericoid endophyte are regulated in this simple but ecologically meaningful way.

Nitrogen mobilization is likely to be crucial to the maintenance of the whole ecosystem since supply of this nutrient to the host is a prerequisite for its own ability to assimilate carbon. The major sink for N in the leaf is the carboxylating enzyme, the functioning of which is rapidly impaired by N deficiency (Field and Mooney, 1986; Read et al., 1989). Release of nitrogen thus enables the completion of a positive feedback loop in which assimilate supplies to the fungus are assured. In addition to nitrogen and phosphorus,there is increasing evidence that the ericoid endophyte can enhance the capture of cations such as calcium (Leake et al., 1990a).

As well as direct involvement in the nutrition of the host plant the activities of the ericoid fungal community produce more indirect benefits. One of the causes of the often exclusive dominance of plants with ericoid mycorrhiza in heathland is that the prevalent acidity gives rise to a 'syndrome' of interacting toxicities involving organic and mineral constituents of the soil which effectively eliminates many plants lacking specialized mutualistic associates. (Jalal and Read, 1983a, 1983b; Read, 1984b). Phenolic and aliphatic acids which are the natural products of decomposition of ericaceous litter occur in their most toxic undissociated form. The ability of *Hymenoscyphus ericae* to assimilate many of the simple organic acids (Leake, 1987) and to absorb metallic ions when these are present at high concentrations (Bradley et al., 1981, 1982) provides protection for the roots of its host plant. Since the roots of would-be competitors that are not so protected fail to penetrate the raw humus of acidic heathland soils (Read, 1984b) it can be construed that the often exclusive dominance of plants with ericoid mycorrhizas under these circumstances is at least in part attributable to the ability of its mycorrhizal fungus to detoxify the environment (Leake et al., 1990b).

## The Ectomycorrhizal Community

The best known and probably most important fungal species involved in the formation of ectomycorrhizal communities are Basidiomycetes. Considerable attention has been paid to changes with time in the populations of the conspicuous above-ground fruiting structures of these fungi (Chu-Chou, 1979; Deacon et al., 1983; Dighton and Mason, 1985) and the results of these studies suggest that under plantation conditions a succession of mycorrhizal fungi takes places, with 'early stage' species, found predominantly in young crops, followed by 'late stage' fungi as the trees mature. Apart from the fact that the functional basis of any such succession is not understood it is important to view extrapolation from fruit body populations to below ground biomass and activity with caution. A detailed study in a plantation of Sitka spruce (Taylor and Alexander, 1990) has shown that over 70% of the spruce mycorrhizas were formed by a fungus, now believed to be *Tylospora fibrillosa* (Taylor and Alexander, 1991), which is not represented in the above-ground population of basidiomes. Species which fruited most abundantly formed less than 5% of the mycorrhizal roots examined. Clearly, we need to examine the mycorrhizal roots and their mycelia directly if we are to understand below-ground processes.

What knowledge we have of the biology of mycelial communities in soil has been derived from two different approaches. In one, exemplified by the studies of Ogawa (1977, 1981, and 1985), field-based analysis of the distribution of vegetative mycelia have been carried out over a number of years. The other approach involves the use of

transparent microcosms in which the development and function of mycorrhizal mycelium can be observed in a non-destructive manner. This technique was pioneered by Skinner and Bowen (1974) using sterile media and later modified to employ unsterile natural substrates (Duddridge et al., 1980; Brownlee et al., 1983; Read, 1984a; Read et al., 1985)

## Ectomycorrhizal Communities in the Field

By careful dissection of the surface layers of soil in forests of Japan, Ogawa (1985) has revealed that there are three basic types of mycelial differentiation in ectomycorrhizal communities (Fig. 2). These are the fairy ring, the irregular mat, and the dispersed colony, each of which has a series of subtypes. Though all of these types are said to be produced by mycorrhizal fungi, closer examination of Ogawa's descriptions reveals that most of the fungi falling into the fairy ring category are, in fact, litter decomposers. Even where 'mycorrhizas' are formed by these fungi, as in the case of the 'shiro' mushroom, *Tricholoma matsutake*, they are said to be of a parasitic kind and to lack a sheath

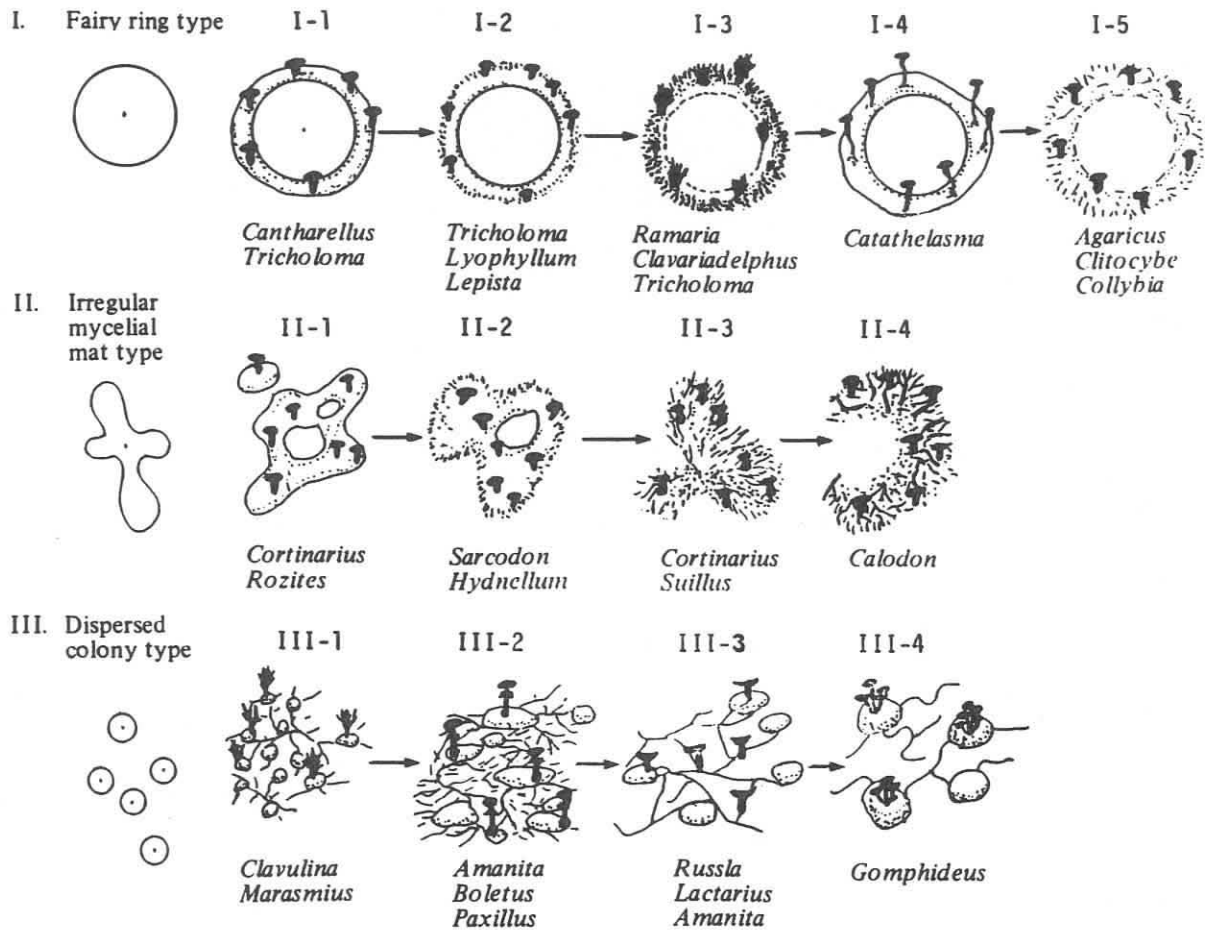



**Figure 2** The three basic types of mycelial differentiation and distribution, with their variants, seen in ectomycorrhizal fungi growing under natural conditions. (From Ogawa, 1985, with permission).

or Hartig net. Diffuse development of undifferentiated mycelium (non-unit restricted growth, sensu Rayner et al., 1987.), may be seen in fungi which utilize continuously distributed nutrient resources such as forest litter.

The fungi of the irregular mycelial mat type include true mycorrhiza formers which show differentiation into mycelial strands or cords, but which form mats restricted to localized areas of intensive development. Within this category almost certainly fall the well defined mycelial mats formed by *Hysterangium* and related species of hypogeous fungi, which can occupy up to 9.6% of the volume of the top 10 cm of soil in Douglas fir forests. (Cromack et al., 1979).

The classic ectomycorrhiza forming fungi of the genera *Amanita*, *Boletus*, *Paxillus*, *Russula* and *Lactarius* form mycelia of the dispersed colony type. Fungi in all of these genera produce vigorous mycelial strands and widely dispersed fruit bodies. It is not known for certain whether vegetative mycelia interlink the dispersed colonies but the extensive nature of the mycelium makes it likely. The pattern of mycelial growth and differentiation seen in this category is typical of that found in fungi whose nutritional resources are discontinuously distributed through the soil. In the case of mycorrhizal fungi the resource units are roots but a similar growth strategy is employed by wood-rotting fungi whose food bases are again irregularly dispersed through the soil (Rayner et al., 1987).

Ogawa's analyses demonstrate that irrespective of 'life type' the mycelia of most of the mycorrhizal fungi are concentrated in the 'F' layers of the forest soil and studies in boreal (Meyer, 1973,) and tropical (Alexander, 1989) forest ecosystems have confirmed that ectomycorrhizal roots themselves are primarily associated with this horizon. While this is evidently the zone in which most of the processes of nutrient mobilization take place some fungi, for example, those producing mats of the *Hysterangium* type proliferate mainly in mineral soil or at the litter-mineral soil interface.

Because of the difficulties involved in obtaining discrimination between the mycorrhizal and other soil communities there have been few analyses of the activities of the mycorrhizal mycelium under field conditions. However, some information on the sizes of genetically distinct ectomycorrhizal mycelia and on the rates of their extension growth in the field has been obtained by determining somatic incompatibility of mycelial isolates from mapped populations of *Suillus bovinus* fruiting bodies (Dahlberg and Stenlid, 1990). A young stand of *Pinus sylvestris* contained a large number (ca. 800/ha) of small clones each spread over a distance of 1–3 m and extending at a rate of up to 20 cm/yr. A nearby mature stand had 25–230 clones/ha, these being up to 30 m across and incorporating several tree root systems. Such observations suggest that selection in favor of some mycelial types occurs at the intra- as well as at the interspecific levels as forests mature.

Where discrete mats of mycorrhizal mycelium occur in mineral soil, as in the case of the Douglas fir—*Hysterangium* association, comparisons can be made between domains occupied or unoccupied by the mycelial mats. Griffiths et al. (1987) observed significantly elevated levels of respiration, and of phosphatase, protease and peroxidase activities in such mats, and later (Griffiths et al., 1990) showed that their respiration rates were most enhanced in spring and autumn. These results suggest investment of carbon by the host to facilitate mobilization of nutrients. While such analyses are of great importance, more precise definition of the activities of mycorrhizal mycelial communities will probably always require manipulation under controlled conditions. Attempts to achieve such definition are described below.

## Ectomycorrhizal Communities in Microcosms

Transparent microcosms maintained under controlled environment conditions (20°C day 15°C night) have been employed to determine the basic kinetics of growth and development of the mycelia of some of the most important ectomycorrhizal fungi. Seedlings, inoculated under sterile conditions with the required symbiont, are transferred, after infection has developed, to thin layers of unsterile acid peat or forest soil between transparent perspex sheets. The progress of mycelial growth can then be followed over months in a non-destructive manner. The patterns of mycelial development differ between fungal species. In some, such as *Cenococcum geophilum* and *Piloderma croceum*, clusters of emanating hyphae develop as restricted outgrowths from each individual root, which do not extend more a few centimeters beyond the root. In contrast the main ectomycorrhizal species in the genera *Amanita, Boletus, Paxillus, Pisolithus, Rhizopogon, Suillus* and *Thelephora* form more extensive systems in which the mycelia from individual roots and even from individual plants merge to form single thalli which ramify extensively through the soil in an integrated manner. Early stages of soil colonization proceed as in the restricted growth category with the production of a dense hyphal mass in the soil around the infected root. This hyphal system moves as a diffuse front at a uniform rate through the soil. Fronts forming from individual roots coalesce to form large fan-like structures advancing through the soil at rates of 2–4 mm day. (Fig. 3).

Similar rates of extension growth have been observed by Coutts and Nicoll (1990a) in mycelial systems of Thelephora terrestris exposed to natural temperatures in summer. They found that growth continued, albeit at a lower rate, throughout the winter (Fig. 4), and also (Coutts and Nicoll, 1990b) that the strands of *Thelephora terrestris* retained viability through long periods of waterlogging. This gives the potential for perennation and the production of a new absorptive mycelium from an established framework of strands in spring.

Mycelial 'cords' or strands form the main lines of communication between the advancing front and the roots of the plant and run through territory which, having been exploited by the advancing front is left largely unoccupied. The only regions behind the front to retain mycelial development are localized 'patches' in which a particular region of the soil continues to be intensively exploited by a diffuse mycelium. Studies in which $^{14}CO_2$ has been fed to the shoots and $^{32}PO_4$ to the mycelia of mycorrhizal plants in chambers containing patches have shown that these are sinks in which carbon and phosphate accumulate (Finlay and Read, 1986a, 1986b).

It is clearly of importance to determine the function of the various types of mycelial structure revealed in such studies. It can be assumed that the primary requirement of the heterotroph is to capture new food bases, which, in the case of mycorrhizal fungi, means infection of new roots. The extensive hyphal front provides an extremely effective mechanism with which to scavenge for such bases and the rapid onset of infection following contact between uninfected roots and the advancing front confirms that the mycelia indeed have a very high inoculum potential. Infection of new roots leads to the formation of communities of interconnected plants in which the ectomycorrhizal fungi provide the potential for direct nutrient transfer between autotrophs at both intraspecific and interspecific levels. (Fig. 5).

This growth strategy is comparable with that seen in many wood decomposing Basidiomycetes in soil where it is assumed to optimize the potential for capture of their irregularly dispersed wood resource units (Rayner et al., 1985). However, the biology of

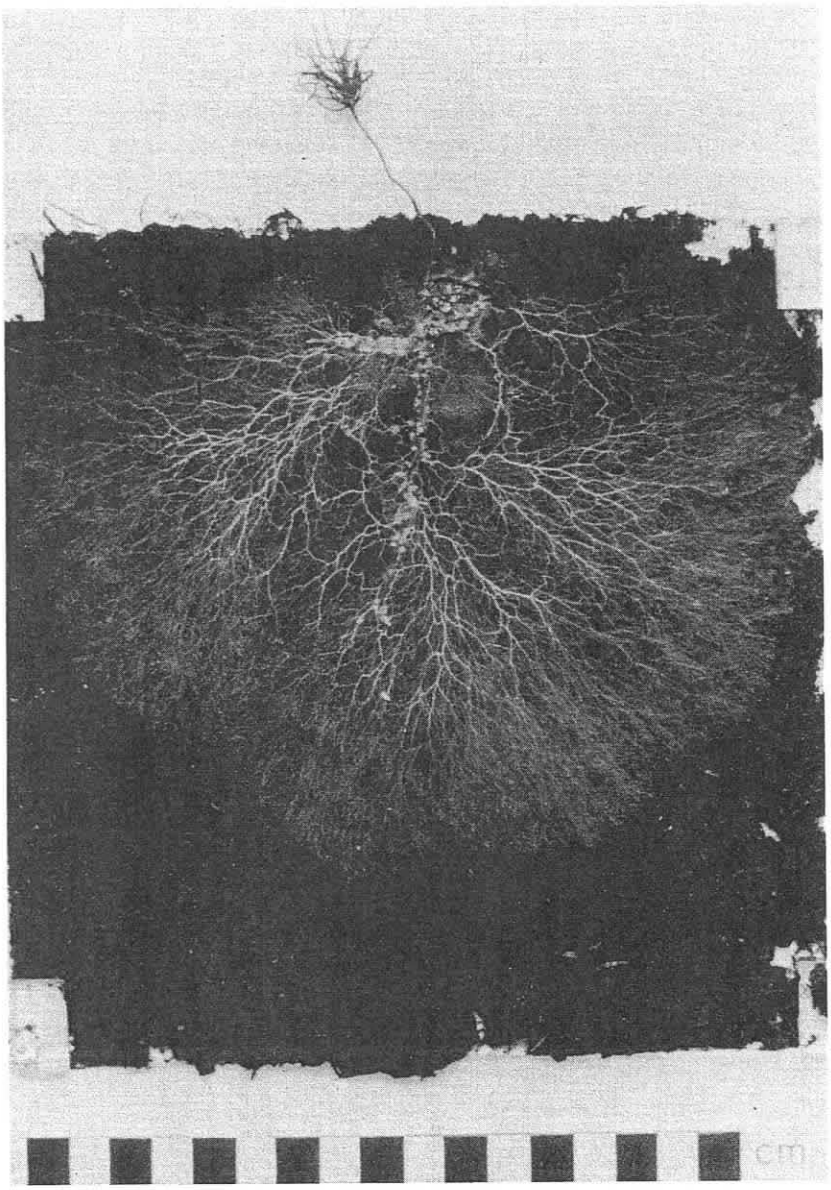


**Figure 3** Mycelial fan of *Suillus bovinus* growing from a mycorrhizal plant of *Pinus contorta* across non-sterile peat. Behind the undifferentiated advancing hyphal front, mycelial stands provide the potential for rapid transfer of captured nutrients to the infected roots.

the mycorrhizal situation differs fundamentally from that of the wood-decomposer in that the requirements of the autotrophic partner must also be considered. Some return on the extensive investment of carbon made by the autotroph (Södertröm and Read, 1987) is required if the association is to be mutualistic. From this point of view the advancing hyphal front can be seen as a structure ideally suited for the capture of mineral nutrients as well as new carbon sources. Studies in observation chambers have confirmed that when $^{32}PO_4$ (Finlay and Read, 1986b) or $^{15}NH_4$ (Finlay et al., 1988) are fed to the advancing mycelial front they are readily absorbed and transported to the

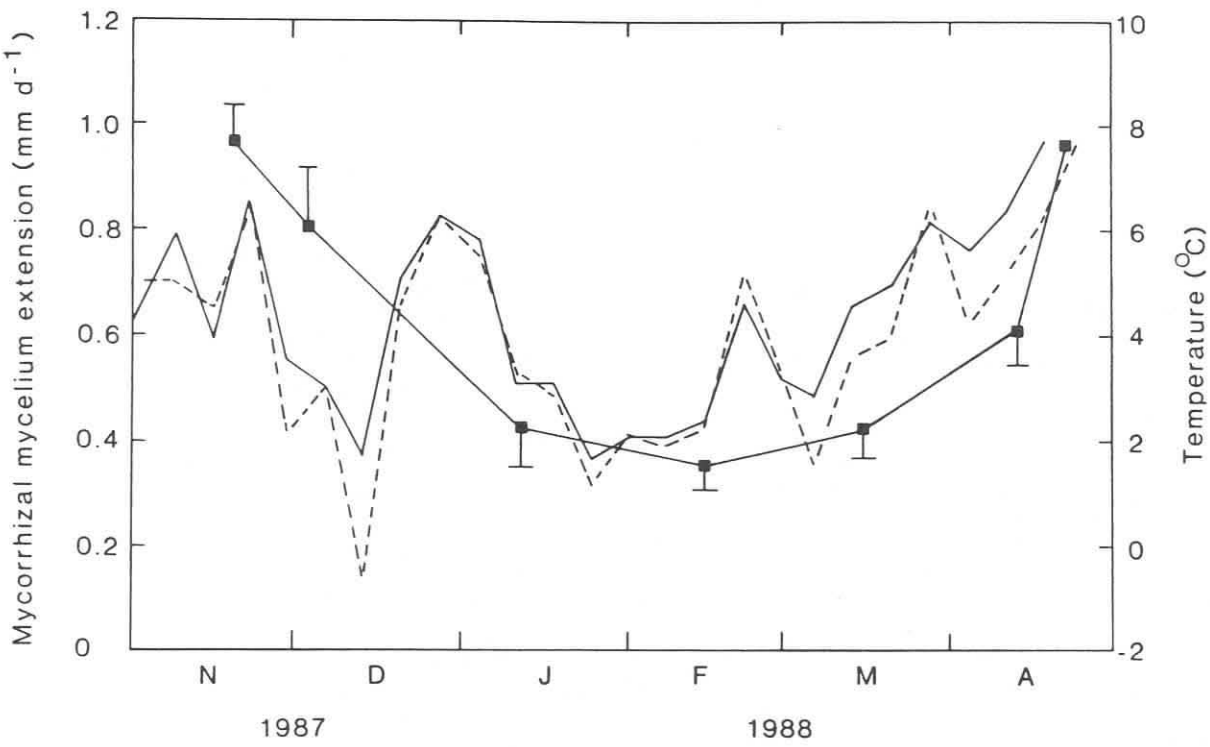



**Figure 4** Mean rates of extension of mycelial fans of *Thelephora terrestris* (closed squares) from November (N) through the winter to April A. Mean (solid line) and minimum (dashed line) temperatures of their environment are also shown. (From Coutts and Nicoll, 1990a with permission).

host. It may have been the requirement for effective mineral nutrient scavenging which, more than any other feature, has caused natural selection to favor as the major ectomycorrhizal associates of plants, those fungi which explore new domains by diffuse growth rather than by means of sharply defined rhizomorphs.

While the ability of the mycorrhizal mycelium to scavenge for mineral nutrient ions is now evident, recent studies, have suggested that it may have an even more fundamental function. It was shown in pure culture studies (Abuzinadah and Read, 1986a) that many of the most widely occurring ectomycorrhizal fungi had the ability to degrade polymeric protein molecules and to use the products of proteolysis, which are almost exclusively amino-acids (Read et al., 1989), as sole sources of nitrogen. In view of the fact that in the forest these fungi, like their counterparts in heathlands, preferentially occupy that domain of the soil in which practically all of the nitrogen is present in organic form, this observation may be of great importance. Subsequent studies have confirmed not only that the nitrogen mobilization seen in pure culture occurs in the mycorrhizal association but also that access of the plant to such resources is entirely dependent upon infection (Abuzinadah and Read, 1986b, 1989).

There is clearly an urgent need to determine the role of the mycorrhizal mycelium in the process of nitrogen mobilization in those organic horizons of forest soils occupied by ectomycorrhizal roots, but studies in microcosms have provided valuable preliminary insights. As part of the experimental analysis of the function of the 'patches' of dense

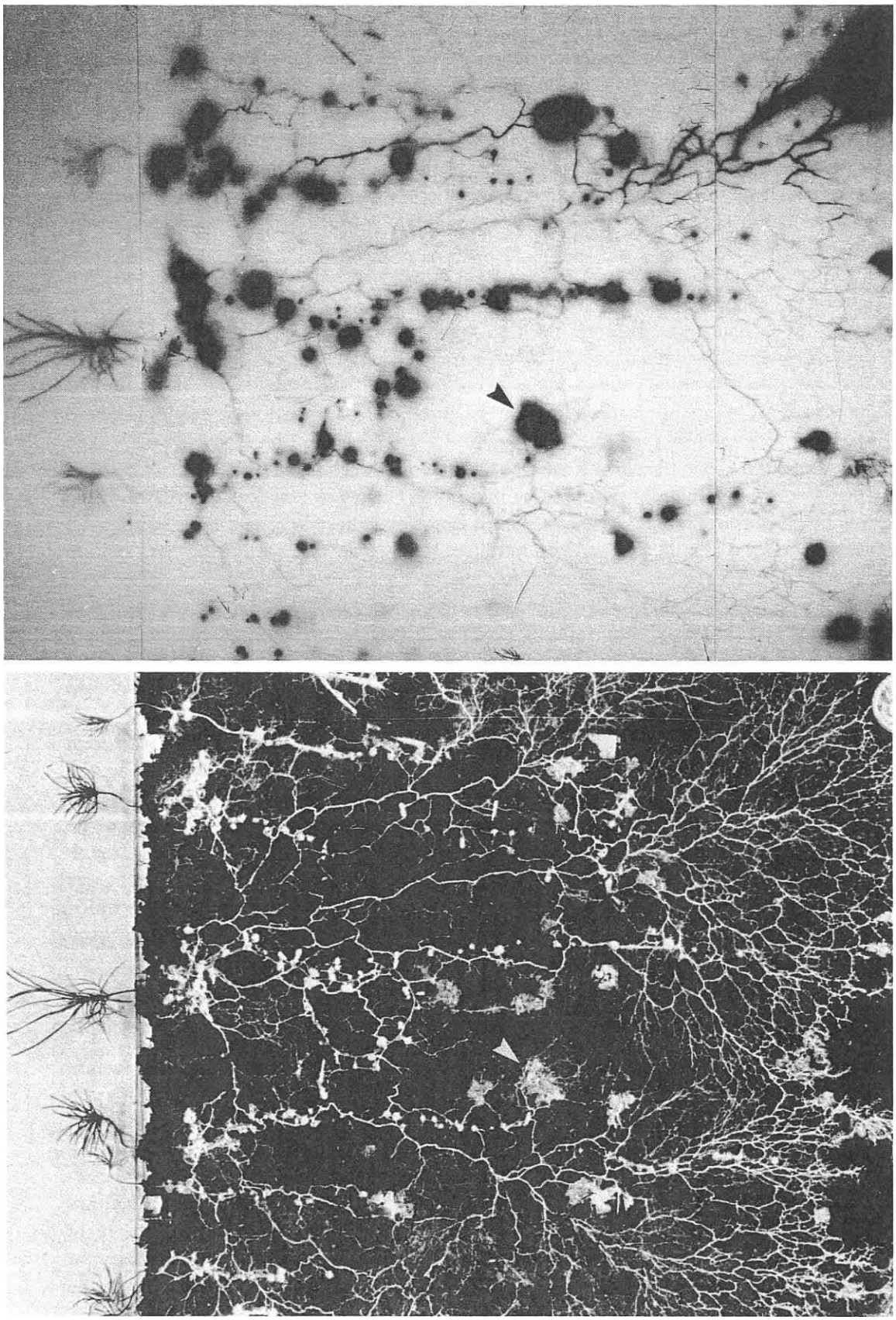
mycelium seen in chambers (Fig. 5) attempts were made to stimulate patch development by adding phosphate and ammonium ions to small areas of the soil immediately behind an advancing hyphal front. When no response was obtained the experiments were repeated using organically enriched materials. Ground or fragmented samples of leaf litter of beech or larch taken from the 'F' horizon of forest soils were placed as discrete blocks in advance of the mycelial front. On contact with these materials intensive proliferation of the fungal mycelium took place and, as the front progressed beyond the blocks, the heavily colonized organic material was clearly identifiable as a 'patch' (Fig. 6).

The first indication that there may be significant amounts of nutrient transfer between the patch and the mycorrhizal seedling was obtained when shoots of these plants, which had been chlorotic prior to 'patch' formation began to regreen. Subsequent analysis of individual needles over a time course on three separate plants provided evidence that their revitalization was a result of nitrogen capture (Read, 1991). The fact that the patches formed in homogeneous soil layers were sinks for, rather than sources of, phosphorus, had already suggested that patch development was associated with something other than P release. The requirement for P, as well as for carbon, in the patches may now be interpreted as indicating a need for energy sources to enable the mobilization of nitrogen. We still do not know that these fungi are directly involved in mobilizing the organic N of the added litter, but we do know from the pure culture studies that they have the biochemical potential to do so.

The recognition of this biochemical potential and of the likelihood that it is expressed when the fungi are grown with natural organic substrates necessitates some reevaluation of the relationship between the ectomycorrhizal fungal community, its host plants and the other microbial communities in the soil. Ectomycorrhizal fungi are no longer seen as being necessarily dependent upon the decomposer community for the provision of access to nitrogen in the form of ammonium or nitrate, but have direct access to the organic residues which are known (Fogel and Hunt, 1983) to be the predominant source of N in forest, as in heathland, systems. Indeed, supplied as they are with photosynthate by their hosts, those ectomycorrhizal fungi with proteolytic capability are likely to compete effectively for organic nitrogen with the other communities. The transfer of nitrogen from litter to host plant by a process not involving the use of carbon from the litter will increase the recalcitrance of the residues, a feature which would explain reduced rates of litter breakdown in the presence of ectomycorrhizal roots observed by Gadgil and Gadgil (1975).

## Vesicular Arbuscular Mycorrhizal Communities

Some of the first communities of land plants appear to have had mycorrhizal infection of the vesicular-arbuscular (VA) type (Kidston and Lang, 1921), and today this is the most widely occurring type of mycorrhizal symbiosis; indeed, the majority of species of land plants are hosts to VA fungi. The infection is produced by a relatively small number of zygomycetous fungi of the genera *Glomus*, *Gigaspora*, *Acaulospora* and *Scutelospora*, which show low host specificity. This type of infection is prevalent in environments in which phosphorus replaces nitrogen as the main growth limiting nutrient of plant communities (Read, 1984a, 1991). While these fungi show a very high affinity for phosphate ions, they appear to have few if any of the other enzymic capabilities of the



(b)

(a)

ericoid and ectomycorrhizal fungi and so are most effective as symbionts under circumstances in which the availability of phosphorus to plants is restricted.

As in the case of the study of ectomycorrhizal mycelial systems, knowledge of the structure and function of VA fungal community has been gained through a combination of destructive field sampling and relatively nondestructive laboratory studies. Examination of the VA mycelium presents even more difficulties than does that of ecto-fungi because it is essentially a more delicate structure. Nonetheless the application of techniques broadly similar to those developed for the study of ectomycorrhizal systems is beginning to reveal that the biology of the two types of community is in many ways comparable.

## Vesicular Arbuscular Mycorrhizal Communities in the Field

While revealing little direct information on the organization of the mycelium in the field, studies of extracted roots and soil samples have provided evidence that the VA mycelium is an extensive structure. Indeed in sand dune ecosystems it has been described as being the main sand binding agency providing for the stabilization of the dunes (Sutton and Sheppard, 1976).

Experiments have been designed to examine the function of the VA mycorrhizal community in the field, but the need to eliminate infection in control treatments presents great difficulties. Attempts to manipulate the mycorrhizal population using the partially selective systemic fungicide benomyl have produced inconsistent results. Application of benomyl to established vegetation can reduce (Fitter, 1986) or have little effect upon infection (Koide et al., 1988), and when infection is reduced there may be no impact upon tissue nutrient concentrations (Fitter, 1986). Since the specificity of benomyl is restricted, its impacts will inevitably be unpredictable.

Other factors combine to reduce the likelihood that application of fungicides to established vegetation systems will provide a sufficiently sensitive means of determining the function of mycorrhizas in ecosystems. Foremost among these is the fact that the nutrient dynamics of those plant communities growing on infertile soils which are most susceptible to mycorrhizal infection, are characterized by seasonal pulses of nutrient mobilization rather than continuous release (Gupta and Rorison, 1975), as well as by an uncoupling of resource capture from growth (Chapin, 1980). It is the essential conservatism of the nutrient economies of those ecosystems most dependent upon mycorrhizal infection which makes them least likely to respond to short term application of fungicide.

Analysis of the development of infection in a grassland ecosystem on calcareous soil (Birch, 1986) has shown that the VA fungal community has a very high inoculum potential, the basis of which lies in an extensive and semipermanent network of mycorrhizal mycelium. Birch showed that pre-imbibed seeds of four of the major herbaceous species of calcareous grassland ecosystem, when placed onto the surface of the soil in the field were infected within 3 to 4 days of radical emergence. The speed and vigor of

**Figure 5a** Group of pine plants grown in non-sterile soil interconnected by the mycorrhizal mycelium of *Suillus bovinus*. Arrow marks mycelial 'patch'.

**Figure 5b** Transfer of phosphate through mycelium to interconnected plants demonstrated by autoradiography of microcosm shown in (Fig 5a). Note accumulation of radioactivity in patches, at the mycelial front and in mycorrhizal roots.

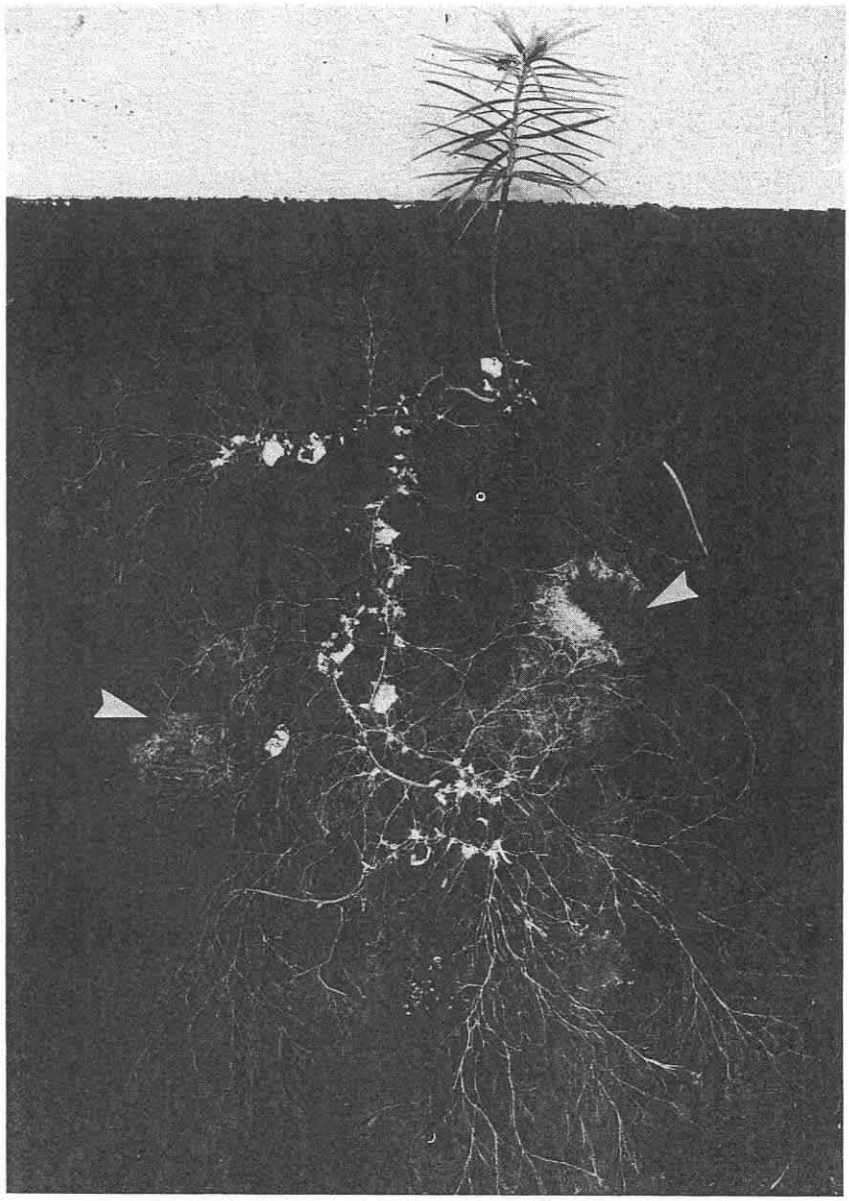


**Figure 6** Microcosm with seedling of *Larix leptolepis* infected with the mycorrhizal fungus *Boletinus cavipes* and growing on a uniform matrix of non-sterile humified forest soil to which litter of *Larix* (left arrow) and *Fagus* (right arrow) has been added in discrete blocks. Note 'patch' development in association with the enriched materials.

the infection is itself sufficient to suggest that spores were not the source of inoculum but wet sieving confirmed that viable spore numbers were extremely low in soil. The low level of host specificity shown by VA fungi is conducive to the spread of infection and to the maintenance of a hyphal network.

The importance of early infection lies in the fact that seedlings germinating in domains already exploited by adult plants gain access to phosphate as their own seed reserves are being exhausted. Read and Birch (1988) obtained evidence that establishment of infection in seedlings was associated with arrest in decline of tissue P concen-

trations as seedlings developed. Enhancement of P inflow at this critical stage in the development of the plant may therefore be of great importance. There is also evidence from agricultural ecosystems that disturbance of the VA mycelium by tillage leads to reduced infection in maize seedlings which, in turn, causes reduction of P inflow and loss of yield (Evans and Miller, 1988). Thus, failure to become incorporated into a closed mycorrhizal community can be a severe disadvantage, especially in the early life of a normally mycotrophic plant.

Allen et al. (1989) examining the response of the non-mycotrophic species *Salsola kali* to the presence of infective mycelium of a VA fungus have highlighted another mechanism whereby a community of compatible mycorrhizal species might be maintained through the activities of the VA mycelium. They found that penetration of roots of *Salsola kali* led to hypertrophic responses at the level of the root and to reduction of vigor of the plants. If widespread, responses of this kind would lead to development of plant communities containing guilds of species which were compatible with and interlinked by a common mycorrhizal mycelium, and to the segregation of these guilds from those containing non-mycotrophic species (Read, 1990).

## Vesicular Arbuscular Mycorrhizal Communities in Microcosms

Considerable advance in our knowledge of the structure and function of the VA mycelium has been provided by the use of observation chambers. Sand has proven to be an ideal medium for such studies because it contains little organic matter and so supports only a small population of saprotrophic fungi. It also has a particle size sufficiently large to enable manipulation. Preinfected plants transferred to shallow transparent dishes of such sand produce an extensive mycorrhizal mycelium most of which is confined to the base of the dish in association with the roots. Its entire structure can be revealed by careful removal of individual sand grains. Such approaches (Francis and Read, 1984; Read et al., 1985) have confirmed that the VA mycelium takes the form of an anastomosing network in which differentiation into the hyphal aggregates seen in ectomycorrhizal systems is largely lacking, but which contains functionally analogous 'arterial hyphae' providing direct connections between resource rich domains be they roots or soil. From these conduits the finer branching hyphae arise. Application of $^{14}CO_2$ to host plants from which such mycelial systems were growing has confirmed that the hyphal network is a living extension of the root system though which carbon fluxes from root to root and even, in the case of interspecific communities of plants, from species to species (Francis and Read, 1984; Read et al., 1985).

Subsequent analyses (Grime et al., 1987) using larger microcosms of dune sand containing mixtures of plant species have confirmed the presence of a vigorous mycelial network and shown that it can have a profound influence upon the structure of plant communities. The high inoculum potential and low host specificity of the VA mycelium provides for rapid infection of compatible species as they germinate and for their incorporation into a large absorptive network, the energy costs of which are largely paid by established plants. Species of plant with small seeds and hence small resources benefit most from infection. A consequence of the effectiveness of the mycelium in scavenging for and colonizing new potential food bases in the form of uninfected roots is therefore to increase the diversity of species in the higher plant community. The evidence thus points to a major role for the VA mycelium in determining ecosystem dynamics both below and above ground.

## Interactions Between Mycorrhizal Communities

Studies of interactions between species with different types of mycorrhiza either when transplanted between ecosystems by humans, or in the naturally occurring transition zones between biomes throw light on the factors determining distribution of mycorrhizal communities. The failure of forest trees, in particular of spruce, to grow in soils dominated by ericaceous plants has long been a matter of concern to foresters. Handley (1963), observing that the roots of these 'checked' trees did not produce normal ectomycorrhizas, sought to explain their poor growth in terms of direct antagonism between the ericoid and ectomycorrhizal fungi. There is, however, no experimental evidence in favor of this contention. In these situations normal ectomycorrhizal development occurs on spruce if nitrogen is added to the soil. It appears to be the failure of the ectomycorrhizal species to compete for nitrogen and thus to complete the carbon feedback loop upon which all mutualistic fungi are dependent, which largely explains the failure of the ectomycorrhizal community in the most extreme mor humus or peat environments. If, after application of N, this loop is completed the ericoid community can in due course be eliminated because its own feedback loop is broken by shade.

The mycorrhizal roots of ericaceous plants form dense mats immediately below the litter layer, (Boggie et al., 1958; Reiners et al., 1965; Gimingham, 1972; Wallen, 1983) in a position analogous to the 'F' or decomposition horizon of forest soils. Here they so extensively exploit that domain of the soil which has the major potential for nutrient mobilization that it effectively becomes dominated by the ericoid community. There is evidence that in order to gain access to nutrients would-be competitors must exploit alternative domains or await the degeneration of the heathland. Thus studies of dry pine-heaths in Scandinavia (Persson, 1980) suggest that ectomycorrhizal roots of pine in the presence of *Calluna* proliferate in a distinct zone below those of *Calluna*. The relatively great sensitivity of many ectomycorrhizal fungi to metallic ions (Burt et al., 1986) and to organic acids may be a factor which restricts their penetration into the most extreme heathland ecosystems and ensures the dominance of the ericoid fungal community.

Where, by whatever means, this dominance is broken, conditions conducive to forest development can occur. The surface litter layers produced by the trees are then extensively exploited by the ectomycorrhizal fungus community. The continuity of this community is ensured by the rapid infection of tree seedlings by fungi growing from the roots of parent trees (Fleming, 1985; Fleming et al., 1986; Newton and Pigott, 1991). The surface horizons of forest soil can thus be occupied by a continuous network of ectomycorrhizal mycelia through which nutrients can pass between trees (Read et al., 1985).

There is evidence to suggest that the quality of the substrates in which they proliferate, often expressed for convenience in terms of C:N ratio, plays a key role in selecting for specific ectomycorrhizal associations within forest systems, as well as in determining the more fundamental patterns of segregation of ericoid, ecto- and VA types of infection on the larger scale. Thus, ectomycorrhizal fungi with better developed proteolytic capabilities in general such as *Amanita, Suillus, Boletinus* and *Paxillus* predominate at the mor-humus end of the C:N gradient while those such as *Pisolithus* which lack such abilities are largely restricted to environments in which C:N ratios are such as to facilitate rapid mineralization of N (Read, 1991).

The same gradient characteristically shows a shift from an understorey with some

ericoid components at the mor humus end to one dominated by species with VA mycorrhizas under conditions where mineralization and nitrification are rapid. A stratification of root development is then often seen (Ellenberg, 1988), roots of ectomycorrhizal tree species being concentrated in the litter horizons at the surface, while those of the herbaceous understory species are largely restricted to the mineral horizons below. This pattern of distribution accurately reflects the different abilities of the ecto and VA mycorrhizal communities to mobilize the nutritional resources of the soil profile. Such segregation of mycorrhizal types has been recorded on a single species of *Eucalyptus* (Reddell and Malajczuk, 1984), the roots of which form ectomycorrhizas in litter and VA mycorrhizas in the mineral soil below.

It is of interest in relation to successional processes that some of the tree species which are prominent at both early and mid stages of primary succession, notably members of the genera *Populus* and *Salix*, can be hosts to VA and to ectomycorrhizal fungi. They thus have the potential to switch from VA to ectomycorrhizal infection as organic matter accumulates with time. The relationships between changing soil conditions and selection for distinctive mycorrhizal communities is particularly well illustrated in the coastal sand dune succession (Fig. 7) in which mycorrhizal fungi influence both the direction and speed of the successional processes (Read, 1989).

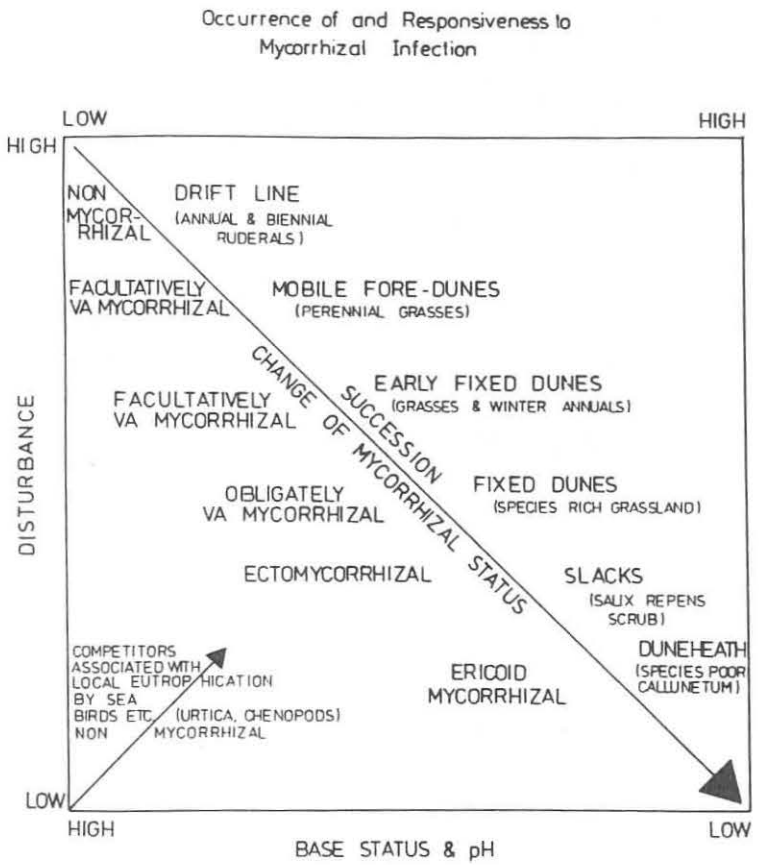



**Figure 7** The succession of mycorrhizal communities seen along an axis representing decreasing disturbance, pH and availability of mineral nutrients as organic matter accumulates in a coastal sand dune succession. (From Read, 1989).

The evidence presented above suggests that in each of those terrestrial ecosystems which have been investigated in depth the dominant plants rely upon the specialized attributes of a distinctive community of mycorrhizal fungi for the capture of those nutrients which most limit productivity. The fungi, in turn, even when possessing some saprotrophic capabilities, are largely dependent upon a direct supply of photosynthate to sustain their growth and to enable the expression of their full biological potential.

There is thus a fundamental interdependence between the communities of mycorrhizal fungi and plants in each ecosystem which eventually determines its structure and dynamics. While we are increasingly aware of the physiological and ecological basis of the interrelationships between these communities we still know virtually nothing of the interactions between the mycorrhizal fungal community and the other groups of soil fungi in these systems. Since methods enabling study of these interactions are now available attention should be given to this challenging area of research.

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